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ACANTHOCEPHALA FROM THE EEL¹

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INTRODUCTION

Because of their migratory habits, eels offer some fascinating problems to investigators interested in the geographical distribution of parasitic organisms. The migrations of most other animals are between places of essentially similar surroundings and for that reason little evidence is available regarding the source of infestations borne by the wanderers. Very little is known of the definite limitations to the distribution of parasites of purely limnetic and terrestrial organisms. On the other hand most of the larger groups of parasitic organisms include species or even genera which are distinctively limited to either a marine or a fresh-water habitat. One of the most interesting and perplexing features of the parasitism of migratory organisms is the fact that they may carry throughout their range mature parasites the larval stages of which have been acquired in a very narrowly restricted locality. Because of the fairly sharp contrast

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between the marine and the fresh-water faunas, organisms like the eel which wander from one to the other offer exceptional opportunity for the study of the influence of migration upon the parasitic fauna of the host. In such migrants it becomes possible to recognize the source of a parasitic infestation with much greater certainty than is possible when the migratory movements are between localities of approximately the same physical environment.

The investigations of Zschokke upon the parasites of salmon stand as probably the most comprehensive work in the literature upon the parasites of migratory fishes. In his studies he included observations upon individuals ascending the Rhine and upon others taken from the Baltic Sea. From the former he recorded twenty species of parasitic worms all of which were apparently acquired by the salmon before they left the ocean. The lack of parasites of limnetic origin is obviously correlated with the fact that all evidence seems to indicate that the Rhine salmon commonly refuses to take food after entering the river. In the Baltic salmon, however, Zschokke found some typically fresh-water species of parasites occurring with the ostensibly marine species. Zschokke's work has been summarized by Ward (1910:1160) in the following manner: "The Rhine salmon shelters a purely marine parasitic fauna, while the Baltic salmon reckons many limnetic forms among its parasitic guests. This remarkable condition finds explanation in the continued feeding of the latter type, even in fresh water, and the resulting enrichment of its parasitic fauna with limnetic forms when it returns to the sea."

Unfortunately, the parasites of the eels have not been investigated as thoroughly as have those of the salmon and little effort has been directed toward interpretation of the isolated observations. In the present paper attention will be confined to the Acanthocephala infesting the eel. A number of investigators have compiled lists of the parasites of the European eel, *Anguilla vulgaris*, but to the present time very little material has been available regarding the Acanthocephala of the North American species, *Anguilla chrysypa*.

Any attempt to determine the origin of the parasitic fauna of the eel must take into account both the pelagic and the limnetic periods in the life cycle of an individual. Regarding the source of infestation of the adult eel found in fresh-water, at least four possibilities must be considered:

1. The parasites may have been acquired in the marine habitat and are retained for a longer or shorter period of time after the host enters fresh-water. If the host remains in fresh-water for a period longer than the life of the individual parasites constituting the original infestation, the intestine would ultimately be freed from its parasites;

2. Eggs or larvae of parasites acquired while the host was in the ocean when discharged into fresh-water may succeed in becoming established in the new habitat through their adaptability to entirely new primary hosts;

3. The parasites may represent an entirely new infestation of typically fresh-water species acquired after the loss of any marine species that might have been carried at the time of leaving the ocean;

4. Marine and fresh-water species may become commingled in the body of the same host individual.

A number of the earlier records of Acanthocephala from *Anguilla chrysypa* have contained apparent misidentifications of species. In some of these instances the present writer has had the opportunity of examining the materials and has found that in one instance of a reputed occurrence of a marine European species from *A. chrysypa* the specimens really belong to a typically fresh-water species probably restricted to North America. In the present paper the writer hopes to analyse the earlier records of Acanthocephala from the eel and to add a considerable bulk of original data which has accrued from the study of several important collections.

MATERIALS AND ACKNOWLEDGMENTS

In the investigation of this problem I have had the privilege of examining specimens and of incorporating data from a number of important parasite collections. Specimens from the U. S. National Museum collected by E. Linton and by A. Hassall have been especially interesting in this connection. Through the courtesy of C. C. Adams specimens secured by H. S. Pratt and F. C. Baker in the course of investigations by the New York State College of Forestry and the U. S. Bureau of Fisheries upon the fauna of Oneida Lake, New York, have been available for study.

In all the writer has examined four species of Acanthocephala from the intestine of *Anguilla chrysypa*, of which one represents a new species described here for the first time. In attempting to make a correct disposition of the species mentioned in the earlier works the writer has been extremely fortunate in being able to examine collections which have verified surmised incorrect determinations and have made corrections in the identification possible.

For data concerning the Acanthocephala of *Anguilla vulgaris* the writer has found it necessary to utilize the published records of European investigators. In a number of instances, where records are the result of compilation from various sources, there are probably errors in the determination of the species. Through the kindness of Professor K. M. Levander of Finland, I have been permitted to study the Acanthocephala encountered in the course of his investigations upon the food and parasites of the eel.

RECORDS OF ACANTHOCEPHALA INFESTING *Anguilla chrysypa*

The first reference to the occurrence of an acanthocephalan in the American eel is that given by Samuel Lockwood in 1872. In a highly entertaining but superficial manner he described a new genus and new species of acanthocephalan from a cyst in the intestine of an eel ascribing to this new form the name *Koleops anguilla*. Unfortunately his description and his figures, based upon the study of a single living specimen, are so generalized that they possess but little of scientific value. Apparently the acanthocephalan from the hog is the only other species of these worms that had ever come to his attention. Both his specific description and his generic diagnosis consist in simple enumeration of a few points of difference between his specimen and "*Echinorhynchus gigas*." All of these differences, with the possible exception of the poorly described proboscis, might apply equally to any one of numerous genera belonging to the family Echinorhynchidae. Consequently both the genus and the species stand as unrecognizable.

Joseph Leidy in his extensive pioneer researches on fish parasites has made no mention of ever encountering Acanthocephala in the American eel.

Edwin Linton, in various reports, has given notice of the occurrence of Acanthocephala in this host. He identified (1889 and 1901) as *Echinorhynchus agilis* specimens which I have determined (Van Cleave, 1913) as *Neoechinorhynchus cylindratus*. Other specimens (1901) he believed to belong to the European species *E. globulosus*. According to his statement these last named specimens were from the collection of the U. S. National Museum. I have examined specimens from this same collection which bear a label indicating that they were identified as *E. globulosus* by Linton and seem to be the same individuals referred to in his paper just cited. A thorough study of these specimens has demonstrated that they represent an undescribed species of the genus *Tanaorhamphus* which is described later in this same paper.

Data concerning the parasites of fishes for A Biological Survey of the Waters of Woods Hole and Vicinity (Sumner, Osborn, and Cole, 1913) were furnished by Linton. Under *Anguilla rostrata* (= *A. chrysypa*) but two species of Acanthocephala were mentioned, namely, "*E. clavaceps* and *E. globulosus*." The first of these is apparently a renaming of what Linton had earlier identified as "*E. agilis*" and what I have more recently shown to be *Neoechinorhynchus cylindratus*.

In the investigation of parasites of fishes from the Illinois River eight eels were examined by the writer (Van Cleave, 1919) but no Acanthocephala were discovered. In addition the writer encountered numerous negative

records as the result of the examination of large numbers of eels taken from salt water at Woods Hole, Mass., during the month of August.

DESCRIPTIONS OF SPECIES

In the light of the present investigation four valid species of Acanthocephala are to be attributed to *Anguilla chrysypa*. Of these one species is new and two of the remaining ones are reported for the first time from this host.

Tanaorhamphus ambiguus n. sp.

Definition. With the characters of the genus. Type female 7.9 mm. long; maximum diameter 0.67 mm.; diameter of posterior region of body about 0.35 mm. Proboscis cylindrical, 0.77 mm. long and 0.19 mm. in diameter, armed with twenty longitudinal rows of about sixteen hooks each. Hooks near middle of proboscis 41 to 47 μ long, with the hook at base of each row about 24 μ long. Proboscis receptacle 0.96 mm. long with wall composed of a single muscular layer. Central nervous ganglion at base of proboscis receptacle. Lemnisci 2.3 mm. long, cylindrical. In the type female each lemniscus contains three giant nuclei. Subcuticular giant nuclei arranged five in mid-dorsal line of body and one in mid-ventral line.

Males have not been studied. Embryos not fully formed in specimens under observation.

Type host: *Anguilla chrysypa*.

Type female collected by Albert Hassall at Baltimore, Maryland, May 30, 1891. This specimen with others of *N. cylindricus* and *E. coregoni* was deposited in the U. S. National Museum under catalog number 6301 of the Hassall Collection. The writer has examined two additional individuals belonging to this same species from the National Museum. These bore the catalog number 6471 and Linton's identification as *E. globulosus*. Neither of these was in as good condition for study as the one selected as type. One specimen, apparently a male of this species, had at some time become dried out and for that reason an accurate determination of internal structure is impossible. Linton (1901:435) states that there are three specimens in the National Museum collection, but it is entirely probable that one specimen was entirely lost at the same time that the damage was done to the male. In the reference just cited, Linton states that this species was numerous in collections made August 7 and 28, 1899.

One of the marked peculiarities of the type of this species lies in the number of nuclei within the lemnisci. All other species of Neoechinorhynchidae from North America examined by the writer agree in possessing two giant nuclei in one lemniscus and one in the other. The lemnisci of the only other specimen of this species are entirely obscured by the develop-

ing egg masses within the body cavity. In figure 5 the three nuclei of one lemniscus are shown while two of those in the other lemniscus occur in the region where the two organs overlap. Until additional specimens are secured for study it is impossible to determine whether this deviation from the customary number of nuclei is an individual abnormality or a character of this species.

But one other species has been described for the genus *Tanaorhamphus* and it is apparently very sharply restricted in its occurrence, having been found in but one host, the gizzard shad (*Dorosoma cepedianum*) from the Illinois River.

Neoechinorhynchus cylindratus (Van Cleave, 1913)

Echinorhynchus agilis of Linton 1889 and 1901

Echinorhynchus clavaiceps of Linton in Sumner, Osborn and Cole, 1913.

Definition. With the characters of the genus. Body almost cylindrical except in immature forms which have the posterior region gradually attenuated. Proboscis approximately globular, slightly broader than long (0.172 by 0.150 mm.), provided with three circles of six hooks each. Hooks of terminal circle 79 to 97 μ long, each bearing a root 58 μ long and 29 μ wide inside the tissue of the proboscis wall. Hooks of middle circle about 37 μ long, without reflexed root. Basal hooks 21 to 25 μ long, simple, thorn-like. Embryos within body cavity of gravid female 49 to 51 μ long and 15 to 21 μ broad.

Specimens collected by Professor Linton at Woods Hole, Mass., were identified as belonging to this species by the writer in 1913 (p. 188). Additional records of the occurrence of this species in the eel have been discovered since that time. Six juvenile specimens were taken from the intestine of an eel from Oneida Lake, New York, in the materials collected by F. C. Baker and H. S. Pratt. Three other eels from the same locality were found to harbor *Acanthocephala* of another species but none of *N. cylindratus*. Two individuals of this species were encountered in an eel examined by A. Hassall at Baltimore, Md., along with the type of *T. ambiguus* and two individuals of *E. coregoni*.

N. cylindratus is distinctively a fresh-water species, the development of which is unknown. Without much question this species gains entrance into the eels after they enter fresh-water. The infrequency of its occurrence in the eel and the lightness of individual cases of infestation would indicate that the eel does not serve as an important definitive host for this species of parasite.

Echinorhynchus coregoni Linkins in Van Cleave, 1919

Definition. With the characters of the genus. Proboscis cylindrical, carrying twelve to fifteen longitudinal rows of ten or eleven hooks each.

Hooks not crowded on proboscis. Basal hooks 28 to 53μ long; those on middle of proboscis 65 to 80μ long; those near anterior tip smaller and weaker than those near middle of proboscis. Ventral hooks slightly larger and stronger than dorsal hooks. Lemnisci not longer than proboscis receptacle. Cement glands of male in a compact mass. Embryos within body cavity of gravid female 51 to 91μ long by 17 to 20μ wide, with an approximately globular prolongation of the middle membrane at each pole.

This species was originally described from the Great Lakes but present indications seem to suggest that its distribution is fairly broad. The writer has recently (1920:6) recorded its occurrence in fresh-water hosts from the arctic regions of this continent. Two individuals of this species were taken from an eel at Baltimore, Md., by Hassall. As indicated earlier in this paper this species was found associated with *N. cylindratu*s and *T. ambigu*s.

Echinorhynchus thecatus Linton, 1891

Definition. With the characters of the genus. Proboscis when fully extended approximately perpendicular to main axis of the body or forming an acute angle with the axis. Proboscis usually about 1 mm. long. Proboscis receptacle long and slender, about 1.5 times the length of the proboscis. Hooks alternate in arrangement; in twelve longitudinal rows of twelve or thirteen hooks each; those at base of proboscis 41 to 53μ long; near middle of proboscis 71μ long; each hook surrounded by a conspicuous cuticular elevation which frequently completely ensheathes the basal hooks of each row. Lemnisci long and slender, about 1.5 times the length of the receptacle. Embryos within body cavity of gravid female 80 to 110μ long by 24 to 30μ broad.

This species is distinctively a member of the fresh-water group. It has been reported from fishes taken from the ocean but these hosts frequent fresh-water habitats. The general outline of the life cycle of this species has been worked out (Van Cleave, 1921) thereby offering additional evidence of its close association with the fresh-water fauna where it occurs as one of the most characteristic acanthocephalan parasites of fresh-water fishes of North America. In the collections from Oneida Lake, referred to above, this species was found in fairly large numbers in the intestine of all of the eels carrying acanthocephalan infestation. This constitutes the first record of the occurrence of *E. thecatus* from *Anguilla chrysypa*.

UNCERTAIN IDENTIFICATIONS

Among the earlier American workers in parasitology there was a marked tendency to ascribe to specimens of Acanthocephala found in American hosts the names of European species. Thus much of the older

literature is replete with instances of the recorded occurrence of European species in American hosts, whereas in the cases that have been investigated carefully it has been shown that with few exceptions the acanthocephalan fauna is distinctively different on the two continents. From point of view of biology and of distribution of the individual species it is extremely desirable that these errors in determination be cited and corrected if possible. In the following section the writer has attempted to analyse some of these older records in the light of more recent investigations.

Neoechinorhynchus agilis (Rudolphi)

E. agilis Rud.

The writer has examined some of Rudolphi's type specimens (Van Cleave, 1919:246) of this species and is confident that all records of the occurrence of this species on the American continent are based upon erroneous identifications. It seems probable that *N. agilis* is rather sharply restricted in distribution to the Mediterranean region.

As indicated previously, Linton (1889 and 1901) identified under this name specimens from the eel which unquestionably belong to the species *N. cylindratus*, the commonest representative of the genus in North American fishes. Furthermore *N. agilis* is a marine species while *N. cylindratus* is definitely associated with the fresh-water habitat.

Kolcops anguilla Lockwood

In the description of this genus and species not a single diagnostic character is given. Characters which are discussed are all contrasted with the conditions found in "*Echinorhynchus gigas*." Apparently this last named species is the only other species of the group with which the describer was acquainted. Supposed peculiarities of the new form are in reality common to all acanthocephalans except members of the family Gigantorhynchidae. Even the drawings are not available as a supplement to the meagre description for no detail of structure, either external or internal, is shown.

"*Echinorhynchus clavaceps*" Zeder

This species has been considered by modern writers as a synonym of *Neoechinorhynchus rutili* (Müller) which infests fresh-water fishes of central Europe. In his later works Linton apparently uses this name to replace his earlier identifications of *E. agilis*. It is highly probable that specimens identified as *E. clavaceps* belong in reality to the species *N. cylindratus*.

Echinorhynchus globulosus Rudolphi

Linton (1901:435) identified acanthocephalans from the eel which were deposited in the U. S. National Museum as belonging to this species.

These same specimens have been found to belong to a previously undescribed species of the genus *Tanaorhamphus* which is described elsewhere in this paper as *T. ambiguus*.

CONCLUSIONS

Four valid species of Acanthocephala are known to occur in the intestine of *Anguilla chrysypa*. All four of these are distinctively American species, of which three are known to occur only in fresh-water fishes. The fourth belongs to a genus which includes but one other species and it is restricted to a single species of fresh-water host. In all of the instances that have been examined carefully there is no evidence of marine species of Acanthocephala inhabiting the intestine of *Anguilla chrysypa*. In this connection a comparison with data from records of infestation of the European eel is interesting.

ACANTHOCEPHALA FROM *Anguilla vulgaris*

Lack of unanimity in determining the synonymy of many species of Acanthocephala infesting fishes makes direct comparisons between records of European investigators extremely difficult. Before the time of Lühe many specific names, the authors of which recognized them as synonyms of earlier workers, had come into very general usage. Thus, for instance, Rudolphi (1802:53) gave the new name *Echinorhynchus angustatus* to *Ech. lucii* O. F. Müller (1778). In spite of this obvious renaming most European workers have, until very recently, failed to recognize the priority of the name *E. lucii* and have continued to use the synonym instead of the valid name of the species. Numerous instances of similar nature are encountered in the literature dealing with the Acanthocephala of fishes. In the following paragraphs names of commonly recognized synonyms have been replaced by the valid names of the species in question.

In his "Register der Acanthocephalen und parasitischen Plattwürmer," Lühe (1911:91) has compiled a list of eighteen species of parasitic worms (exclusive of nematodes) which have been recorded from the eel in central Europe. Only six of these are recognized as strictly marine, while all seven species of the Acanthocephala included in his list are typically fresh-water forms with the possible exception of the encysted larvae of an undetermined species of the genus *Corynosoma*.

K. M. Levander (1909) in his admirable contribution to the knowledge of the food and parasites of the fishes of Finland has utilized the names current in the literature for the species of Acanthocephala encountered in his investigations. His data upon the parasites of *Anguilla vulgaris* include three species of Acanthocephala from this host. Since the time of the publication of his work the names *Echinorhynchus angustatus*, *E.*

globulosus, and *E. claviceps* have become recognized as synonyms of *Acanthocephalus lucii* (Müller), *Ac. anguillae* (Müller), and *Neoechinorhynchus rutili* (Müller) respectively. Professor Levander very kindly sent me specimens from *Anguilla vulgaris* and I have been able to confirm his determinations with changes to the valid forms of the names mentioned above.

Porta (1905) listed nine species of *Acanthocephala* from the eel of which two, *Echinorhynchus gadi* and *Acanthocephalus propinquus*, are supposedly of marine origin. However, Porta's records in this work are the result of promiscuous compilation and it is entirely possible that either or both of these species have been misidentified.

The following table gives some of the more important contributions to the knowledge of the acanthocephalan fauna of the European eel.

TABLE I
Acanthocephala Reported from *Anguilla vulgaris*

Species	Porta 1905	Lühe 1911	Levander 1909	Stossich 1885-1898
<i>Neoechinorhynchus rutili</i>	+	+	+	
<i>Acanthocephalus lucii</i>	+	+	+	+
<i>Acanthocephalus anguillae</i>	+	+	+	
<i>Acanthocephalus propinquus</i>	+			+
<i>Echinorhynchus gadi</i>	+			
<i>Echinorhynchus clavula</i>	+	+		
<i>Echinorhynchus lateralis</i>	+			+
<i>Echinorhynchus salmonis</i>		+		
<i>Pomphorhynchus laevis</i>	+	+		
<i>Echinorhynchus miliaris</i> (encysted)	+			+
<i>Corynosoma sp?</i> (encysted)		+		

In the above table are listed eleven species of *Acanthocephala* from *Anguilla vulgaris*. Two of these are larval forms thus leaving nine species as recorded from the intestine of this host. One of these nine species, *A. propinquus* is restricted to marine fishes while another, *E. gadi*, is considered by European investigators as a typically marine species which is brought into fresh-water only through the agency of migratory fishes. Thus of the species of *Acanthocephala* infesting *Anguilla vulgaris* two are apparently acquired during the marine phase of its existence and the remaining seven are introduced into the intestine of the eel while it is an inhabitant of fresh-water. From the foregoing it will be seen that the two species of eel differ not only in regard to the species of *Acanthocephala* harbored but likewise differ in the origin of their infestations. The *Acanthocephala* of *Anguilla chrysypa* seem to be entirely of fresh-water origin

while those of *A. vulgaris* comprise a mixture of marine and fresh-water species.

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EXPLANATION OF PLATE

Each figure is accompanied by a scale which indicates the magnification. The scales accompanying figures 3 and 5 have the value of 1 mm., all others on this plate represent 0.05 mm.

All figures were drawn from stained whole mounts in damar with the aid of a camera lucida.

Fig. 1. Profile view, portion of a single row of hooks from proboscis of *E. thecatus*, showing characteristic cuticular prominence around each hook.

Fig. 2. Proboscis of *N. cylindricus*, surface view, showing characteristic arrangement of hooks.

Fig. 3. Female of *E. coregoni* showing general arrangement of organs. Note especially the lemniscus (*l*) which is shorter than the receptacle of the proboscis (*r*).

Fig. 4. Embryo from body cavity of female of *E. coregoni* from *A. chrysopa*.

Fig. 5. *Tanaorhamphus ambiguus*, type female, showing general arrangement of organs: *b*-brain, *c*-egg mass, *l*-lemniscus, *n*-subcuticular giant nucleus, *r*-receptacle of the proboscis.

Fig. 6. Proboscis of type female of *T. ambiguus*.

